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Lethal trap created by adaptive evolutionary response to exotic resource

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Global transport of organisms by humans provides novel resources to wild species that often respond maladaptively. Native herbivorous insects have been killed feeding on toxic exotics, which acted as "ecological traps[1-4]." We document a **novel** trap stemming from the opposite effect, high fitness on an exotic resource despite lack of adaptation to it. *Plantago lanceolata* was introduced to Western North America by cattle-ranching. Feeding on this exotic plant released a large, isolated population of the native butterfly *Euphydryas editha* from a longstanding tradeoff between maternal fecundity and offspring mortality. Because of this release, and despite reduced insect developmental rate on the exotic, *Plantago* immediately supported higher larval survival than the insects' traditional host, *Collinsia parviflora*[5]. Prior work in the 1980's documented evolving preference for *Plantago* by ovipositing adults[6]. We predicted that, if this trend continued, the insects could endanger themselves, since availability of *Plantago* to butterflies is controlled by humans, and humans change management faster than butterflies evolve[6]. Here we report fulfillment of this prediction. The butterflies abandoned *Collinsia* and evolved total dependence on *Plantago.* The trap was set. In 2005 humans withdrew their cattle, springing the trap. Grasses grew around the *Plantago*, cooling the thermophilic insects, which went extinct. This extinction could have been prevented if the population had retained partial use of *Collinsia,* which occupied drier microhabitats unaffected by cattle removal. The flush of grasses abated quickly, rendering the meadow once again suitable for *Euphydryas* feeding on either host, but no butterflies were observed from 2008-2012. In 2013-4 the site was naturally recolonized by *Euphydryas* feeding exclusively on *Collinsia*, returning the system to its starting-point and setting the stage for a repeat of the anthropogenic evolutionary cycle.

Subject terms: *Euphydryas,* eco-evolutionary dynamics, anthropogenic evolution, conservation, exotic host, ecological trap, insect diet, host shift, oviposition preference, evolutionary trap.

Main The late Gary Polis described *Homo sapiens* as a "ubiquitous keystone pest[7]." And so we are[8]. Although adaptation to human activities allows some wild species to coexist with us[9], many fail to adapt to human land management and suffer in consequence. An example is the setting by humans of "ecological traps[10,11,"] defined as follows: "in an environment altered suddenly by human activities, an organism makes maladaptive habitat choices based on formerly reliable environmental cues, despite availability of higher quality habitat[11]."

Most ecological traps result from preference by wild organisms for novel resources that are unsuitable or toxic. Australian monitor lizards suffered population crashes after feeding on toxic exotic cane toads[12]. Bees maladaptively preferred crops grown from seed treated with neonicotinoid insecticides[13]. Several examples involved insect herbivores feeding on exotic hosts that reduced insect fitness[1-4] but fell short of causing population extinctions, because traditional hosts were still used alongside the exotics.

In the "ecological trap" scenario the novel resource is accepted as food, but is initially detrimental[11], with the expectation that evolution should lead either to behavioural avoidance of the resource or physiological ability to use it[3]. Here, we describe a different type of trap formed by a novel resource that immediately supported such high fitness that a butterfly population evolved complete dependence on it, causing local extinction when humans withdrew our apparent gift. This paradoxical phenomenon is previously undescribed and doesn't fit published definitions, either of "ecological trap" or "evolutionary trap[1,11]."

Our study insects, the thermophilic[14] Edith's checkerspot butterflies, *Euphydryas editha*, formed a sedentary, isolated population around the margins of a spring-fed meadow, Schneider's Meadow, at 1800m elevation in Carson City, Nevada. They have one generation per year. Their novel host was the exotic perennial, *Plantago lanceolata,* and their traditional host the ephemeral native annual *Collinsia parviflora* (Extended data Fig. 1).

The geographically closest *E. editha* populations of the same ecotype as Schneider, but where *Plantago* had not arrived, used *Collinsia* as their sole host[5]. When neonate larvae from one of these "ancestral" populations were transplanted to Schneider, their survival on *Plantago* was identical to that of the local Schneider insects[5]. The "ancestrals" were ready to use *Plantago* from the moment of its introduction. It is not surprising, then, that this exotic has been colonized twice by other North American *Euphydryas*[15,16]. Oregon *E. editha taylori* are now

dependent on the exotic, though it is not clear if this is due to evolution of the butterfly, since the original host(s) have disappeared[16].

During the 1980's, survival of *E. editha* at Schneider was consistently higher on the exotic than on the traditional host (Table 1), despite larval growth being c.18% slower on *Plantago*[5]. Where the principal host is ephemeral, as is *Collinsia*, female *E. editha* face a trade-off between maternal fecundity and offspring survival. Prolonging larval development can increase fecundity, but the resulting delay in adult emergence augments the risk of offspring mortality from host senescence[17]. The evolutionary response to this trade-off has been to delay emergence to the point where many offspring routinely starve from phenological asynchrony with their hosts[17]. The stage is set for the time constraint to be released and fitness increased by host-switching to the longer-lived *Plantago*, despite slower larval growth on it. Indeed, the majority of larval mortality observed on *Collinsia* was from host senescence, while *Plantago* did not senesce during the seasons of larval activity.

No adult females sampled from "ancestral" populations preferred *Plantago* over *Collinsia* for oviposition, but around 20% accepted both hosts equally[5]. In contrast, by 1982 *Plantago* was already preferred for oviposition by a minority (c.7%) of preference-tested adults at Schneider[6]. Evolution of *Plantago* preference had begun.

Given natural selection for oviposition on *Plantago*, and given that oviposition preferences at Schneider were both heritable (estimated heritability 0.9) and correlated with offspring performance[18], we expected to see rapid evolution of preference. We did: the proportion of insects preferring *Plantago* increased to around 50% by 1990[6]. This change was heritable. Laboratory-raised, *Collinsi*a-fed offspring of field-caught 1990 butterflies were significantly more *Plantago*-preferring than similarly-raised offspring of field-caught 1983 insects[6].

Here, we report that the bout of anthropogenic evolution continued until monophagy on *Plantago* was achieved. In 2005 and 2007, all tested females preferred to oviposit on the exotic (Fig. 1a) and in 2007 all larvae found in the field were on *Plantago* (Fig. 1b). The insects had abandoned both their traditional host, *Collinsia*, and the minor host, *Penstemon rydbergii*, that had been incorporated into their diet during the host shift (Extended data Table 1, Extended data Fig. 2).

In 1993 we wrote that this episode of anthropogenic evolution was “foreshadowing a new problem in Conservation Biology. By adapting genetically to human-induced changes, the insects risk becoming dependent on continuation of the same practices. This is a serious risk, because human cultural evolution can be even faster than the rapid genetic adaptation that the insects can evidently achieve." [6]

This prediction was fulfilled. In late 2005, following the death of "Uncle Harry" Schneider, the meadow was sold and cattle-grazing ceased. Grasses grew freely. By March 2007, 96% of *Plantagos* had become embedded in grass (Table 2, Extended data Figs. 3,4a) and *E. editha* larvae wandered among dense vegetation, no longer able to bask in sunlight on bare ground adjacent to their hosts.

The conspicuous communal webs spun by gregarious young larvae render *E. editha* easy to census (Extended data Fig. 4b) and population extinction feasible to establish. Searches for larval webs, eggs and adults found no *E. editha* in 2008, 2009, 2010 or 2012 (Fig. 1c, Extended data Table 1). The population was extinct.

By analogy with known cause-effect relationships involving other thermophilic butterflies, we attribute this extinction to the flush of lush vegetation caused by cattle removal. Lushness is associated with high rates of predation on butterfly larvae[19] and increased lushness caused by abandoning of traditional management in Europe has caused ground-level cooling resulting in butterfly declines and local extinctions[20-22]. The UK extinction of the Large Blue butterfly was attributed to lushness-caused microclimatic cooling, following myxomatosis-related reduction of grazing by rabbits[22]. Restoration of grazing and re-warming of ground-level microclimate were essential for this butterfly's successful re-introduction[22].

Particularly in sparse vegetation, sunshine creates thermal stratification with microclimate hotter close to the ground[23], speeding insect development[24]. We used prior observations of natural ovipositon sites at Schneider to measure "eggspace" temperatures. Eggspaces on exposed *Plantagos* were augmented by 13.4°C above ambient, compared to 6.0°C on embedded *Plantagos*, leaving "eggs" on embedded plants >7°C cooler, on average, than those on exposed plants (Extended data Table 2). In light of the high proportion of plants embedded in 2007 (Table 2), and of the known adverse effects of host embedding[16,19] and

153 microclimatic cooling[20-22] on other butterflies, it is not surprising that this cooling was
154 followed by extinction.
155
156 As anthropogenic nutrients were used up, the flush of grasses abated naturally in 2008, since
157 when *Plantagos* exposed to full sunlight have again been available (Table 2, Extended data
158 Fig. 5). In 2013-4 butterflies recolonized: an exhaustive search in 2014 revealed nine *E.*
159 *editha* larval webs, all on the ancestral host, *Collinsia* (Fig.1b,c, Extended data Fig. 4b).
160 Recolonization had occurred from a population resembling the starting condition, prior to the
161 anthopogenic evolution.
162
163 The distance from Schneider's Meadow to the nearest known population of the subspecies,
164 *E.e. monoensis*, at Simee Dimeh summit, is 37.7km. How far is this to a *Euphydryas?*
165 Harrison[25] measured colonizations of empty habitat patches by the Bay Checkerspot (*E.*
166 *editha bayensis*) and found that the greatest cumulative distance travelled in ten years was
167 4.5km. Given this sedentary nature of the butterfly and the physical isolation of the meadow,
168 we did not consider the possibility of rapid recolonization. Our mindset in 2014 was simply
169 to reconfirm the extinction and we were astonished to find larvae. After the event, we
170 discovered that the "Carter Springs" fire in September 2012 had positively impacted the
171 Simee Dimeh butterflies, dramatically extending size and lifespan of *Collinsia* (Extended
172 data Fig. 6), resulting in a population boom of *E. editha* similar to previously-documented
173 response to fire[26] and providing a plausible source of *Collinsia*-feeding *E. editha* despite the
174 distance.
175
176 Could the original population have survived if it had retained its traditional diet of *Collinsia*
177 alongside *Plantago*, as it did from 1982 to 2002? *Collinsia* was both most abundant and most
178 used by the insects in dry sagebrush around the meadow edge (Extended data Figs. 1,2,3),
179 where removal of cattle did not result in embedding of *Collinsias*, even at peak lushness in
180 2007 (Table 2, Extended data Fig. 3). If the butterflies had adopted the exotic less
181 completely, they would likely have survived the change of land use. Conversely, if they had
182 remained monophagous on *Collinsia* they may not have survived the bottleneck in 1988-9[6],
183 when, after record-breaking frost without insulating snow (-25°C at Minden on January 1,
184 1988), the population was spatially restricted to a small, sheltered, south-facing area from
185 which *Collinsia* was coincidentally absent (Fig. 1b,c; discussion with extended data Fig. 2).
186

Evolution of *E. editha* at Schneider illustrates the process by which, long ago, European grassland butterflies evolved widespread dependence on human haymaking and grazing, rendering themselves vulnerable to abandonment of traditional management techniques[20-22]. However, *E. editha* as a species is not threatened by the trap we document. Its ecotypic variation and rapid evolution augur well for resilience to environmental fluctuations, whether natural or anthropogenic[23]. In contrast, substantial perturbation occurred at the subspecies level, since *E. e. monoensis* is currently restricted to four known sites: two isolated populations and two metapopulations distributed along 235km of the eastern Sierra Nevada from McGee Creek at latitude 37.29 to Schneider at latitude 39.11.

Unless the Schneider population sent out successful propagules, which we judge unlikely, the lineage we observed from 1982-2007 is extinct. At the population level, the changes we observed exemplify dramatic, oscillating anthropogenic evolution of a species not directly targeted by humans. This example of small-scale oscillating diet evolution oddly mimics repeated recolonizations of abandoned hosts detected across millions of years by phylogenetic analysis of the butterfly family Nymphalidae, to which *E. editha* belongs[27].

Attempts at "evolutionary rescue" of wild species[28,29] may be compromised when anthropogenic traps such as that documented here remain undetected. These traps may be cryptic to humans, but understanding them may become increasingly important to species conservation in the Anthropocene.

Data availability. Raw data are included in the Figure, Tables and Extended data.

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Author Contributions Both authors participated in field censuses and writing. MCS performed oviposition preference tests and statistical analyses.

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Figure 1. Changes of *E. editha* oviposition preference (a), larval diet (b) and population density (c). The two preference graphs (a) are not mirror-images because insects without preference are not shown. Changes in strength of preference are shown in Extended data Fig. 7. (b) absence of larvae on *Collinsia* in 1988-89 caused by temporary spatial restriction during and after bottleneck; in those two years larvae were restricted to *Plantago* and *Penstemon* (extended data Table 1 and extended data Fig. 2). Numbers within graphs represent biologically independent sample sizes; individual adult insects (a) or larval groups (b,c). Error bars = 95% c.i. calculated according to Newcombe[31], with continuity correction; source data in Extended data Table 3. No error bars for larval diet in years of inadequate sampling (1982, 1983, 2015) or total census (1988,1989, 2014).

346 **Table 1. Survival of *E. editha* placed in the field on *Collinsia* and *Plantago* at**
347 **Schneider's Meadow in the 1980's.** Proportions of groups surviving analyzed as 2x2
348 contingency tables by Fisher's exact test, two-tailed.

Year And reference	Life Stages measured	Group Survival *Collinsia*	Group Survival *Plantago*	Individual survival *Collinsia*	Individual survival *Plantago*	Statistical significance (group survival)
1980 (previously unpublished)	Oviposition to second instar	33% (n = 15)	70% (n = 20)	Not recorded	Not recorded	P = 0.044
1982[30]	Oviposition to second instar	17% (n = 58)	55% (n = 86)	4% (n = 1810)	24% (n = 2764)	P = 0.000011
1985[5,18]	Larval survival for ten days from hatch	62% (n = 63)	84% (n = 62)	19.9% (n = 1260)	27.1% (n= 1240)	P = 0.0085 (combining data from both references)
1986 (previously unpublished)	Oviposition to second instar	29% (n = 28)	80% (n = 25)	Not recorded	Not recorded	P = 0.00028

349

350 **Table 2. Estimated host densities and percentages of each host embedded and exposed.**

Year	*Plantago* density, plants/m^2	*Collinsia* density, plants/m^2	Percent *Plantago* embedded	Percent *Collinsia* embedded
1984	2.3 (50 in 244x 30cm quadrats	103 (2266 in 244x30cm quadrats	<10%	<5%
2005	9.4 (317 in 15 x 2.25 m^2 quadrats)	27.5 (330 in 12 x 1m^2 quadrats)	<10%	<5%
2007	0.21 (18 in 85 x 1m^2 quadrats)	35.2 (528 in 15 1m^2 quadrats)	96.4% (189/196)	10.5% (69/657)
2008	2.8 (44 in 16 x 1m^2 quadrats)	26.1 (418 in 16 x1m^2 quadrats)	18.6% (43/231)	13.8% (77/559)
2009	2.5 (48 in 19 x 1m^2 quadrats)	45.7 (869 in 19x 1m^2 quadrats)	11.8% (251/2115)	11.7% (114/975)
2014	3.4 (173 in 50 x 1m^2 quadrats)	52.4 (472 in 9 x 1m^2 quadrats)	8.5% (28/328)	18.0% (150/833)

351

352 **Methods**

353

354 **Statistics.** All tests are two-tailed. Error bars on Figures, given only where justified by
355 sampling techniques, are 95% c.i., calculated by vassarstats.net, using methodology of
356 Newcombe[31] for c.i of proportions, with continuity correction. Figure 1a does not explicitly
357 depict insects without preference but they can be deduced by subtracting the depicted
358 percentages from 100%. Otherwise no relevant data have been omitted from any experiment
359 or set of observations. Sample sizes were largely limited by feasibility.

360

361 **Data availability.** Raw data are included in the Figure, Tables and extended data.

362

363 **Blind preference testing.** Oviposition preference tests to estimate heritability[18] were
364 performed blind, in the sense that the tester did not know which insects were sibs or offspring
365 of particular parents. The high heritability estimate from this blind testing (0.9) gave
366 confidence that the tests were not subject to severe observer bias; repeated blind testing of the
367 same butterfly by different observers has also given confidence. However, in the present MS
368 the appropriate blind test would require the tester to not know which year it was, and we were
369 not able to achieve this without compromising the quality of the data.

370

371 **Figure 1a.** Butterflies were captured in the field and their oviposition preferences tested by a
372 standardized technique, in which encounters are staged between the tested insect and each
373 plant in alternation. Plants were undisturbed in their natural habitats or freshly transplanted
374 into pots in their own soil. Acceptance of plant taste was judged from full abdominal curling
375 and extrusion of the ovipositor for 3 sec[32]. Acceptance and rejection were recorded at each
376 encounter, but oviposition was not allowed[32]. Videos showing acceptance in such staged
377 encounters are in reference 24. During each test the range of plants that would be accepted, if
378 encountered, expands over time with increasing motivation to oviposit. Therefore, acceptance
379 of plant A followed by rejection of plant B is recorded as preference for A over B. Testing of
380 assumptions underlying this technique described in reference 32. Because insects without
381 preference are not shown in the Figure, percentages do not sum to 100% except in 2005 &
382 2007, when preference for *Plantago* was unanimous among tested butterflies. Raw data are in
383 Extended data Table 3. A more detailed comparison between early and late periods, showing
384 strength as well as direction of preferences, is given in Extended data Fig. 7. The assumption

385 that these insects' preferences are not influenced by prior experience, either as larvae or as
386 adults, is supported by prior observation and experiment[18,32,33].
387
388 **Figure 1b.** Percentages of egg clutches/larval groups found on *Plantago*. Raw data in
389 Extended data Tables 1 and 3. Low sample sizes in 1988 and 1989 were total counts,
390 reflecting bottleneck. High proportion of larvae on *Plantago* in 1989 reflects lag in
391 recolonization of *Collinsia* after spatial restriction in bottleneck, shown in Extended data Fig.
392 2. In 2002-2007 we searched a larger area for larvae on *Collinsia* than for larvae on *Plantago*.
393 For those years the Figure, showing the proportion of larvae found on the two hosts,
394 overestimates the overall proportion on *Collinsia;* the areas searched are in Extended data
395 Table 1. To be conservative we indicated data for 2002 and 2005 as "published" although
396 neither sample sizes nor confidence limits were given previously[33]. The graph shows that in
397 2015 we found a single group of hatching eggs on *Collinsia.* However, we performed no
398 census in 2015, our visit was too early.
399
400 **Figure 1c.** Estimates of density of larval webs, on all hosts combined, per 10,000m^2. Raw
401 data in Extended data Table 1. In each census, individual host plants of all species were
402 searched for eggs, larvae, larval webs and typical damage. Very different scales of census
403 were conducted in different years. For small patches, every individual host plant could be
404 searched, for larger patches, stratified line transects were used. Confidence limits are not
405 given, but the log scale of the Y-axis makes clear the dramatic scale of population changes;
406 for example, the raw data (Extended data Table 1) include the finding of 34 groups in only
407 70m^2 in 1982 and 4 groups in 20,000m^2 in 1988. No density estimate is given for 2007,
408 because, although 38 groups were found (Fig. 1b), at the time of the last census some were
409 still eggs, so harder to find than larvae. Sample calculation for 2002, (see methods for
410 Extended data Table 1): estimated number of webs on *Plantago* = 67 x 4,000/170 = 1576.
411 Total number on *Collinsia* = 3 (all were counted). Estimated total number webs in entire area
412 of 20,000m^2 = 1579; density per 10,000m^2 = 789.
413
414 **Table 1.** Effects of oviposition host on fitness: eggs were placed out on randomly-chosen
415 hosts in the field, by manipulating butterflies to lay (videos in ref. 24). Gregarious neonate
416 larvae were placed out with a sable brush in groups of 20-35. After ten days of larval life, just
417 before diapause, each group was gathered in. It is in pre-diapause life that the principal

418 effects of oviposition on fitness are manifest, since post-diapause larvae are mobile and can
419 switch between host species.
420
421 **Table 2.** Host densities estimated from quadrats along line transects placed randomly within
422 the strata of the ecotone where each plant was concentrated (Extended data Fig. 1). Early
423 rough estimates of percent embedded from photographs, memory and anecdotal observation,
424 since embeddedness was uncommon and its value as a trait was not anticipated prior to the
425 sudden embedding of *Plantago* in 2007. A plant was classed as "embedded" if surrounded for
426 > 50% of circumference by vegetation taller than itself. In most cases the differences between
427 "embedded" and "exposed" plants were striking (Extended data Fig. 3); in the March census
428 in 2007 some embedded plants were hidden and not found, pressed under thatch from winter
429 snow, inaccessible to post-diapause larvae feeding in March but reappearing and, if no longer
430 completely embedded, accessible to ovipositing butterflies in May. Extended data Fig. 4a has
431 a photo of eggs naturally laid on such a reappearing *Plantago*, emerging from winter thatch,
432 in May, 2007.
433
434 **Extended data Table 1.** Table contains counts over wider areas including lower host
435 densities than the "core areas" censused in Table 2. Total area where suitable *Plantago* might
436 be found was around 4,000m^2 ; total area that might contain suitable *Collinsia* was larger,
437 maximally about 17,000m^2 (1982 map in Extended data Fig. 2) but less in dry years. About
438 1,000 m^2 overlapped between the two distributions. Wider areas were searched in 1988 and
439 1989 to check whether we had missed part of the population in prior work. We had not, so
440 since we found no habitat in wider search, subsequent searches were restricted to meadow
441 margins and adjacent sagebrush, approximately 20,000m^2 (Extended data Figs.1 & 2).
442
443 In 2002, 2005 and 2007 the entire area where larvae might have been found on *Collinsia* was
444 searched, but *Plantago* areas were not searched in entirety, merely sufficiently to get an
445 estimate of plant density and occupancy by the butterflies. After the extinction in 2007-8, the
446 entire habitat was searched in each census. In most years, more plants were searched for *E.*
447 *editha* than were included in censuses to estimate plant density reported in Table 2.
448
449 The Table shows data from areas censused in which plants with and without larvae were
450 counted. Where maps in Extended data Fig. 2 show more insects than the Table, as in 1982,

451 the insect distribution in the map is derived from rapid assessment in which insects were
452 observed and counted but plants were not.
453
454 **Extended data Table 2.** Eggspace temperatures were measured with a fine thermocouple
455 (MT-29/1B insect probe, type T, copper-constantan). After measuring each exposed *Plantago*
456 we measured one or two adjacent (within 1m) embedded plants growing in the same position
457 within the ecotone; we took care that embedded plants were not systematically growing in
458 more humid microsites. When two embedded plants were measured, we used the mean value
459 of the two for analysis.
460
461 We found three errors in our prior publications: (1) number of groups found on *Collinsia* in
462 1990 is here corrected to 18 from 6[6]; (2) number of butterflies preference- tested in 1986 is
463 corrected from 31 to 36[5,6]; (3) misleading early reference to population as feeding on
464 *Plantago* in 1969[34] stemmed from initial visit in June, after *Collinsia* had senesced and
465 disappeared. Faster-growing larvae on *Collinsia* had entered diapause and were not found,
466 while some still remained feeding on *Plantago.* Next visit in 1971 made clear that, although
467 *Plantago* was already being used, *Collinsia* was the principal host. No censuses were
468 performed in 1969-71.
469
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Extended data Figure 1. **Habitat and host distributions at Schneider's Meadow**. **a:** Butterfly habitat is a single, isolated, spring-fed wet meadow in the centre of the picture, surrounded by non-habitat for the butterflies: dry sagebrush scrub and coniferous forest. **b:** Distribution in the meadow-edge ecotone of the principal hosts, *Plantago lanceolata* and *Collinsia parviflora*, plus the minor host *Penstemon rydbergii*. **c:** Typical difference in phenology between *Plantago* and *Collinsia* in May 2014. In the foreground are red, senescent Collinsia plants that are edible to the insects but will die within a few days; behind them is a single green, budding *Plantago* that will remain edible until after all *E. editha* larvae have entered diapause. **d:** Hatching egg clutch on *C.parviflora* cotyledon in hot, dry microhabitat.

Extended data Figure 2. **Changes in distribution of early stages of *E. editha* (eggs or larvae) from 1982-2007.**

Data added by hand to GoogleMaps image. Most stars represent several groups. For example, in 1989, 23 groups were found on *Plantago* and one on *Penstemon*. The restricted distribution in that year followed a bottleneck in 1988 after record-breaking cold in January, without the usual insulating snow cover. Schneider's Meadow is at 1700m elevation. Nearby towns at lower elevations recorded -25C on January 1 1988 (Minden, 1444m elevation) and -20C on January 18 (Carson City, 1424m). Note recolonization of *Collinsia* as the insects expanded back into the distribution of *Collinsia* in 1990 and 1993. Larval groups recorded in 1988 and 1989 were clustered around an attractive nectar source (*Wyethia* sp.); it is possible that adults attracted to this nectar in 1988 had survived as larvae on *Collinsia* in 1987-8, then laid eggs in 1988 on *Plantago* adjacent to nectar. This possibility prevents us from making a definite conclusion that the population would have become extinct if eggs in 1987, prior to the bottleneck, had been laid only on *Collinsia*. Data for 2005 exist, and closely resemble those for 2002.

Extended data Figure 3. **Effects of cessation of grazing: *Plantagos* embedded, *Collinsias* unaffected.** Data in Table 2. Panel **a** shows a *Plantago* at Schneider in 1984, exposed to full sunlight and physically acceptable to ovipositing *E. editha.* Panel **b** shows the meadow edge in May 2007, after cattle removal. In the foreground is *Plantago* habitat with thick grasses; in the background is *Collinsia* habitat not grassed-in, with barren spaces between the sagebrush. Panel **c** shows Collinsia parviflora in May 2007, unaffec ted by the embedding that simultaneously affected the Plantagos shown in panels **d** and **e.** Embedding in grasses not

only cooled the *Plantagos* (Extended data Table 2) but rendered them hard to find, both by butterflies seeking oviposition sites and by larvae seeking food.

Extended data Figure 4. **a. Natural egg clutch laid in May 2007 on *Plantag*o**
The plant is pushing through winter thatch, and would have been unlikely to be acceptable to ovipositing butterflies prior to cattle removal, when plants like the one in Extended data Fig 3**a** were available. **b. Communal web spun after recolonization**. Second-instar larvae on *Collinsia* at Schneider in May 2014. This is a single group of larvae probably stemming from a single oviposition event; there were 9 such groups, all on *Collinsia.* Oddly, this group is not on the most exposed *Collinsia* available.

Extended data Figure 5. **The return of mostly-exposed *Plantagos* after anthropogenic lushness abated.** Photos taken in 2014, but Table 2 shows that they could have been taken in 2008 or subsequently.

Extended data Figure 6. **Effect of fire on size and longevity of *Collinsia parviflora***.
A single fire-enhanced *Collinsia parviflora* individual at McGee Creek (East of Bishop, California) is still blooming. There is a small web of *E. editha* larvae at its base from a naturally-laid egg clutch. The fifteen senescent individual *C. parviflora* lying on the ground are a haphazard sample gathered from unburned microsites within 2m of the enhanced individual.

Extended data Figure 7. **Strength and direction of oviposition preferences of butterflies sampled at Schneider in 1983 and (2005+2007).**
The number over each bar is the sample size of biologically independent samples: individual butterflies captured in the field. The "discrimination phase" is the length of time for which the insect would search, during which it would consistently accept the preferred host and consistently reject the second-ranked host. At the end of this phase, if it does not succeed in ovipositing, the insect enters an "acceptance phase," after reaching the level of oviposition motivation at which either host would be accepted, whichever were next encountered.

Insects in the blue 1-4 column on the left of the Figure would search for 1-4 hours during which only *Collinsia* would be accepted. If they failed to find *Collinsia* within 4 hours, they would subsequently accept either host, until actual oviposition occurred. Green central bar

shows butterflies without preference. Sample size for 2005-7 is smaller than in Fig.1a because we include on Fig.1a (and here omit) 5 butterflies for which we determined the direction of preference, but not the strength.

Extended data Table 1**. Census results: areas searched and numbers of egg clutches or larval webs found on each host.** Data for 1982-1993 from reference 6. These are not the same data shown in Extended data Fig. 2; see Methods. Extension of survey to 50,000m^2 in 1989 did not reveal additional habitat, so density in Fig.1c for that year is calculated using the estimated maximum habitat area of 20,000m^2, giving a higher estimate than reported in reference 6.

Extended data Table 2. **Measurements of temperature excess over ambient air at 1m height at three potential types of oviposition site at Schneider's Meadow: embedded *Plantago*, exposed *Plantago* and exposed *Collinsia*.**
Measures taken at eggspace height (2-4cm) between noon and 15:00 in May 2015. Each measure of exposed *Collinsia* or *Plantago* came from a different, haphazardly chosen habitat patch. On occasion we measured two embedded *Plantagos* in the same patch; when this occurred we show the mean of the two values and used those means in analysis, treating the two plants as a single sample. Consequently, each data point in the Table represents a biologically independent sample, and the independent sample sizes are 12, 18 and 18 as indicated at the base of each cell.

Comparison between exposed *Plantago* (mean excess 13.4) and embedded *Plantago* (mean excess 6.0) by two-sided t-test: $t = 7.55$, $df = 28$, $p < 0.0001$
Comparison between exposed *Collinsia* (mean excess 11.46) and exposed *Plantago* by two-sided t-test: $t = 1.77$, $df = 28$, $p = 0.09$

Extended data table 3. **Source data for means and confidence limits of adult preference and larval diet, shown in Fig. 1a,b.** Statistical test described in caption to Fig.1.